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Saccadic Eye Movement Conjugation in Children

F. FIORAVANTI,*† P. INCHINGOLO,* S. PENSIERO,‡ M. SPANIO§

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In recent years the conjugacy of the saccadic eye movements has been studied extensively in adult humans, while little investigation has been carried out in children. We studied the characteristics of binocular saccades in school-age children, finding significant differences with adults, particularly in their dynamics and binocular coordination. The largest deviations were found in the youngest children. An incomplete optimization of the saccadic waveform and a poor disconjugate compensation of the mechanical asymmetries of the plants are hypotesized to explain the results.

Saccades Children Main sequence Post-saccadic drift

INTRODUCTION

Saccadic eye movements are generated by a combination of phasic and tonic activity in the motoneurons. It is generally assumed that the pulse components are produced by a burst of neuronal firing with the goal of compensating the viscous forces produced by the muscles, while the step components are tonic changes in the discharge rate required to counteract the elastic forces produced by the orbital tissues and the muscles that hold the eye in the final position (Robinson, 1975).

In normal adult humans, the matching of the pulse and step components is responsible for the accuracy of the dynamics of the movement. In case of mismatching, a post-saccadic drift motion of the eye towards the final position is produced. If the pulse is too small, the eye will drift onwards; if too big, the drift will be in a backward direction.

Even though the pulse-step of innervation is normally assumed to be sent equally to both eyes, according to Hering's law (Hering, 1868), the presence of asymmetrical post-saccadic drift in the two eyes has frequently been reported by many researchers (Collewijn, Erkelens & Steinman, 1988; Lemij & Collewijn, 1991a,b, 1992; Kapoula, Optican & Robinson, 1989). Moreover, the disconjugate drift compensation behaviour of the system has been tested in some studies, particularly in presence of strong asymmetrical weakening of the muscles (Inchingolo, Optican, Fitzgibbon & Goldberg, 1991), but also with pure visual stimulation (Kapoula, Hain, Zee & Robinson, 1994; Kapoula, Optican & Robinson, 1990; Kapoula, Eggert & Bucci, 1994). Both the origin of the disconjugacy of the post-saccadic drift (different mechanical properties of the two plants, different pulse-step matching in the two eyes etc.) and the disconjugate adaptive properties of the system have mainly been studied in adult humans and primates, while little investigation has been done in children until now (Accardo, Pensiero, Da Pozzo & Perissutti, 1992; Aslin & Ciuffreda, 1983; Dannermiller, Banks, Stephens & Hartmann, 1983; Hainline, Turkel, Abramov, Lemerise & Herris, 1984). In the present study we have investigated the main characteristics of binocular saccades in school-age children (5–13 yr), in order to point out the enhancement, if any, of the saccadic binocular co-ordination and conjugacy during growth.

METHODS

Subjects

Binocular eye movements were recorded in 12 children aged between 5 and 13 yr (mean age, 9.25 yr) and four adults (mean age, 31.25 yr), as reported in Table 1. All subjects were normal, and none of them had a history of ocular or oculomotor pathology. No refractive anomalies were present and visual acuity was 10/10 in each eye for all the subjects. Both children and adult subjects were naive as to the purpose of the experiment. All subjects had good binocular vision, as ascertained by the Bagolini striated glasses test for binocularity and random-dot test for stereopsis.

Recording technique

Eye movements were recorded from both eyes on the horizontal plane by using a prototypal wide-range

*Dipartimento di Elettrotecnia, Elettronica ed Informatica, University of Trieste, Via Valerio 10, 34100 Trieste, Italy.
†To whom all correspondence should be addressed [*Email* fioravan@gnbts.univ.trieste.it].
‡Div. Oculistica, Children's Hospital "Burlo Garofolo"-34100 Trieste, Italy.
§Clinica ORL, University of Trieste, Via Valerio 10, 34100 Trieste Italy.

infrared limbus-tracking system (Accardo, Busettini, Inchingolo, dell'Aquila, Pensiero & Perissutti, 1989), connected to the local area network. The head of the subject was fixed by means of a chin and forehead support and by a dental bite bar. The arrays of infrared emitters and sensors (two for each eye) were mounted on the support and were accurately pointed to the limbus of the eyes by means micrometric adjustments; during this procedure, a cross-shaped light beam was projected from each array to the eyes, revealing the position of the emitters. The system allowed the recording of horizontal eye movements in a range up to 60–70 deg (from 30–35 deg to the left to 30–35 deg to the right).

After low-pass filtering at 100 Hz with a three-pole Butterworth filter and a digitalization at a sampling rate of 500 Hz with a resolution of about 1 min arc in the central quasi-linear field (primary position of each eye), the data were stored on UNIX workstations connected to the network, where they were processed and analysed off-line.

Since the eye position is non-linearly related to the detected signal with infrared techniques, a non-linear offset and gain correction must be applied to the left-eye and right-eye channels. The two correction functions were accurately evaluated by applying a fourth-order polynomial interpolation on the fiducial fixation samples recorded during a calibration session of 50 saccades with monocular vision with the right and the left eye. During this session the non-viewing eye was patched. Each function was checked over time, to discover and quantify possible offset artifacts due to lateral or retrobulbar displacements of the eyes, or to an imperfect blockage of the subject's head. The correction functions were finally compared with analogous functions obtained by fitting three cycles of ± 30 deg sinusoidal smooth pursuit tracking, repeated at the beginning and at the end of a saccadic test session. A couple of corrective look-up tables, one for each eye, was generated by inverting each function, and used to linearize all the data-records. Any value of the infrared limbus-tracking outputs associated to more than one eye position in the look-up tables or statistically affected by excessive relative error, was marked on the reconstructed eye traces, signalling the unavailability of the data.

Experimental procedures

Visually-driven horizontal saccadic eye movements were elicited by jumps of 5–25 deg in size (with steps of 5 deg) on an isovergence LED circle, in a range from 20 deg to the left to 20 deg to the right. Each session consisted of 70 target jumps, with a randomized timing in the range 0.9–1.2 sec. The LED circle was placed at a distance of 1 m from the subject. The starting position, the amplitude and the direction of the jumps were randomized. Subjects were allowed some practice and the data recording started when they felt ready.

Data analysis

The recordings have been analysed by computer programs developed on UNIX platform. The detection of primary saccades was performed by a velocity criterion of 15 deg/sec. Saccades having an amplitude less than 30% of the target displacement were discarded. Velocity was calculated by a FIR differentiator of length 6, applied with the time-reversal technique to avoid the introduction of a time delay. The frequency response of the filter was tested with digital computer simulations. All the saccades associated with blinks were automatically rejected. According to Collewijn *et al.* (1988) and Lemij and Collewijn (1989), the saccade offset was marked by detecting the decrease of velocity below 15 deg/sec, and the minimum saccadic pulse duration was set to 15 msec. For each primary saccade the estimated parameters were: (i) saccade amplitude; (ii) saccade duration; (iii) peak velocity; (iv) rise time; (v) skewness (acceleration phase duration ÷ total saccade duration).

The position error at the end of the saccade [pulse position error (PPE)] and at the end of the post-saccadic drift [step position error (SPE)] were computed by subtracting the target position from the eye position. Since corrective saccades could occur before the end of the drift, all the movements with secondary saccades were not included in the evaluation of the SPE (27% of the total number of saccades).

Post-saccadic drift was analysed by considering the eye movement starting 20 msec after the end of the primary saccade and lasting 400 msec. The 20 msec gap was adopted to reject the occasional dynamic overshoot, as well as very small time constant components. The identification of post-saccadic drift time-constants was performed by fitting the eye position trace with a double exponential (two time constants), since this procedure allows a better estimation of the main time constant when more than one component is present; only the time constant of the larger amplitude component was finally considered. The fitting was realized with an adaptive least-mean-square algorithm.

Secondary saccades were detected with the same velocity criterion used for primary saccades, but minimum and maximum time delay from the offset of the preceding primary saccade were set to 50 and 300 msec respectively.

The vergence trace was defined as the difference left − right eye position: therefore convergent angles were positive and divergent angles were negative.

TABLE 1

	Children												Adults			
Subject	GS	LR	MD	GD	MM	GG	LM	MC	VP	CC	IB	AM	GP	MT	MM	DF
Sex	F	F	M	M	F	F	M	F	M	M	M	M	M	M	F	M
Age (yr)	5	6	6	7	8	9	11	11	11	12	12	13	25	26	35	39

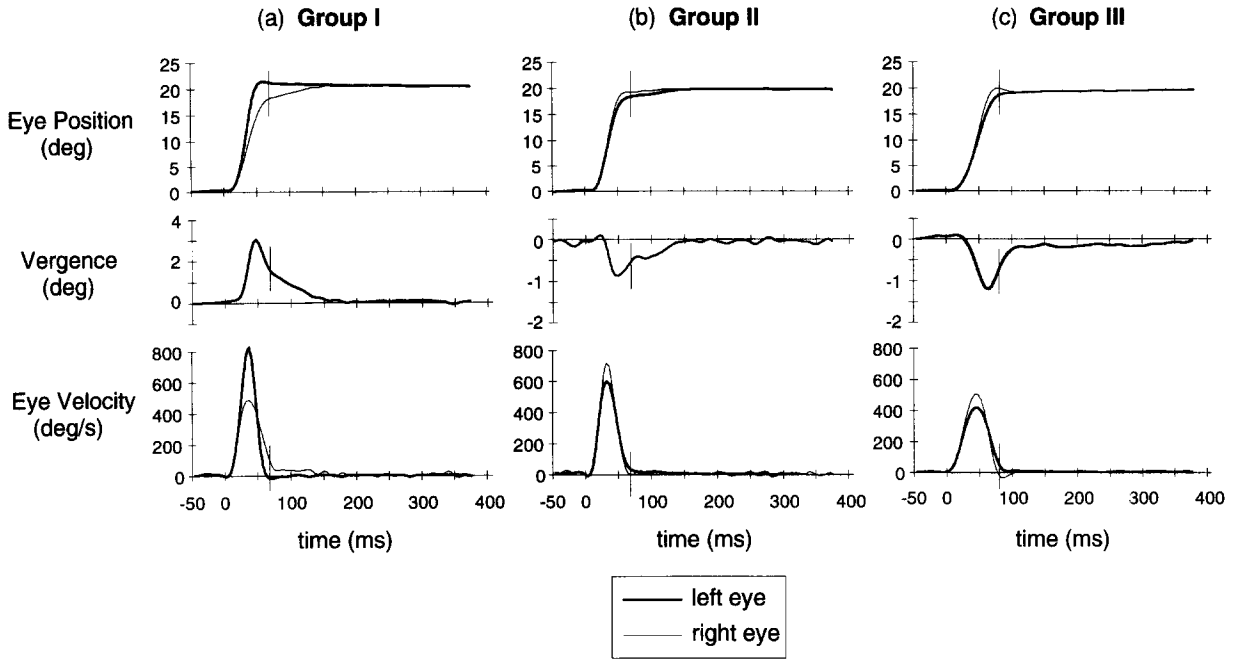

FIGURE 1. Position (upper graphs), vergence (middle graphs) and velocity profiles (lower graphs) of typical binocular saccades for three subjects. (a) Subject MD, 6 yr old. (b) Subject VP, 11 yr old. (c) Subject DF, 39 yr old. The vergence trace is the difference LE − RE.

In order to perform an accurate binocular analysis and to point out the differences in the response of the two eyes, the analysis of the main saccadic parameters (peak velocity, drift amplitudes, time duration etc.) was run separately for the two eyes, marking the time events on the velocity trace of the eye being tested. Only in the case of the vergence analysis the marking of the starting instant of the drift was run on the cyclopean eye trace, defined as the average of the right and left eye position traces.

The final data analysis was computed by grouping the subjects by age as follows: group I included children from 5 to 10 yr (six subjects); group II included children from 11 to 13 yr (six subjects); group III included adult subjects (four subjects). The splitting of the children into two age groups was initially suggested by the opposite sign of the intra-saccadic vergence change, which was shown to be reversed in very young children with respect to older children and adults; the significance of this grouping was therefore confirmed by the statistical analysis of the data. To validate the recording system and the data analysis procedures, the data from the adult subjects were compared with the minimum and maximum values reported in other studies (Boghen, Troost, Daroff, Dell'Osso & Birkett, 1974; Baloh, Sills, Kumley & Honrubia, 1975; Schmidt, Abel, Dell'Osso & Daroff, 1979; Abel, Troost & Dell'Osso, 1983; Fuchs & Binder, 1983; Collewijn *et al.*, 1988), where similar paradigms and saccade detection techniques were used. Our test recordings on adults fit in well with most of these results. The statistic significance of the differences between the three age groups was verified with a multivariate analysis of variance (MANOVA), and the requirement of homogeneous variances was verified with the test of Bartlett. The degrees of freedom for each group were 15 for the comparison between the two children's age groups and 10 when the adult group was also considered. The requested level of significance was always > 0.01.

RESULTS

Intra- and post-saccadic vergence

The effects of saccade disconjugacy normally introduce a transitory vergence change during horizontal saccades, although no vergence change is required by the target. This effect has been largely studied in adult humans and originates from the different timing and amplitude of the peak velocity in the two eyes. In normal adult humans, the amplitude and the peak velocity of the abducting saccade are larger than those of the adducting one (Collewijn *et al.*, 1988), producing a net divergence at saccade offset (Collewijn *et al.*, 1988; Kapoula *et al.*, 1994; Zee, Fitzgibbon & Optican, 1992). The correct vergence angle is usually recovered with a slow post-saccadic convergent drift.

In this study, the sign of the intra-saccadic vergence at the saccadic offset changed with the age of the subjects. Very young children, from 5 to 9 yr old (group I), showed positive (convergent) intra-saccadic vergence changes; older children, from 11 to 13 yr old (group II) and adults (group III) showed negative (divergent) intra-saccadic vergence changes. The amplitude of the changes in the vergence angle will be analysed in the next paragraph.

The effect of asymmetries between temporal and nasal saccades is shown in Fig. 1, where the position, velocity and vergence profiles for three subjects belonging to different age groups are reported. In Fig. 1(a) (subject MD, 6 yr old), the adducting saccade made by the left eye has larger amplitude than the abducting saccade of the right eye, producing a positive net vergence change at the

saccade offset. Moreover, the shorter duration of the acceleration phase and the larger peak velocity of the adducting saccade contribute to generate the positive vergence peak.

In Fig. 1(b) (subject VP, 11 yr old), the sign of the intra-saccadic vergence change is negative, indicating that the asymmetries between adducting and abducting saccades in older children are reversed with respect to those observed in young children. In this case, in fact, the abducting saccade is larger than the adducting one and also has higher peak velocity. This produces a net divergent change at the saccade offset. This behaviour was observed also in adult subjects [Fig. 1(c), subject DF, 39 yr old], in agreement with the results reported in previous studies by other researchers.

Disconjugacy of binocular saccades

The disconjugacy of the saccades made by the two eyes was analysed by evaluating the difference left eye − right eye for the following local parameters: saccade amplitude, peak velocity, duration and acceleration time. The data were grouped by target amplitude and by saccade direction, i.e. separating leftward and rightward saccades. For each of the analysed parameters, a marked difference was observed between abducting and adducting saccades.

Figure 2(a) shows the saccade disconjugacy, i.e. the difference in the size of the saccades made by the left eye and the right eye. For group I, the positive values of the difference in the case of rightward saccades and the negative ones for leftward saccades indicate that the saccades of the abducting eye are significantly smaller

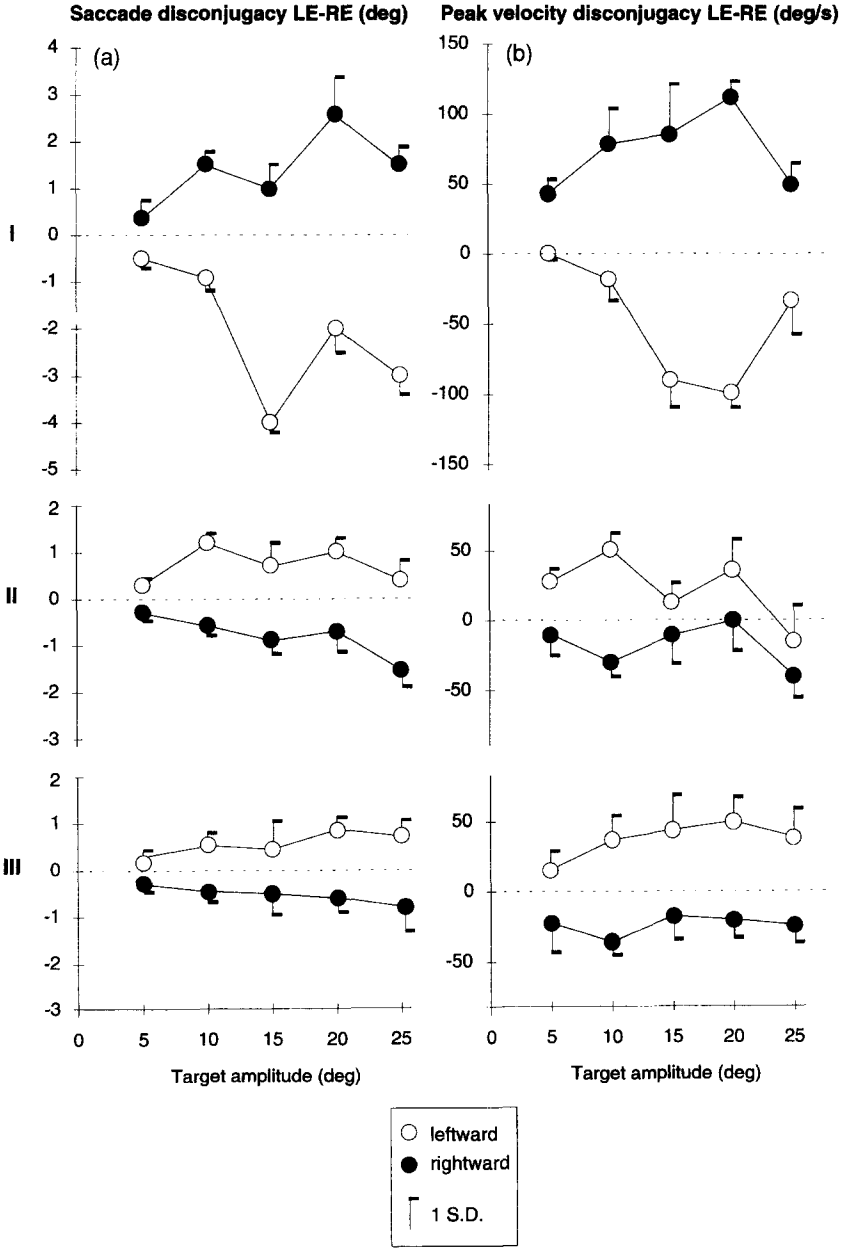

FIGURE 2. Saccade disconjugacy (a) and peak velocity disconjugacy (b) of the saccades for groups I, II and III. Saccades from the two eyes were pooled together, but rightward (●) and leftward (○) directions are shown separately. Vertical bars indicate 1 SD.

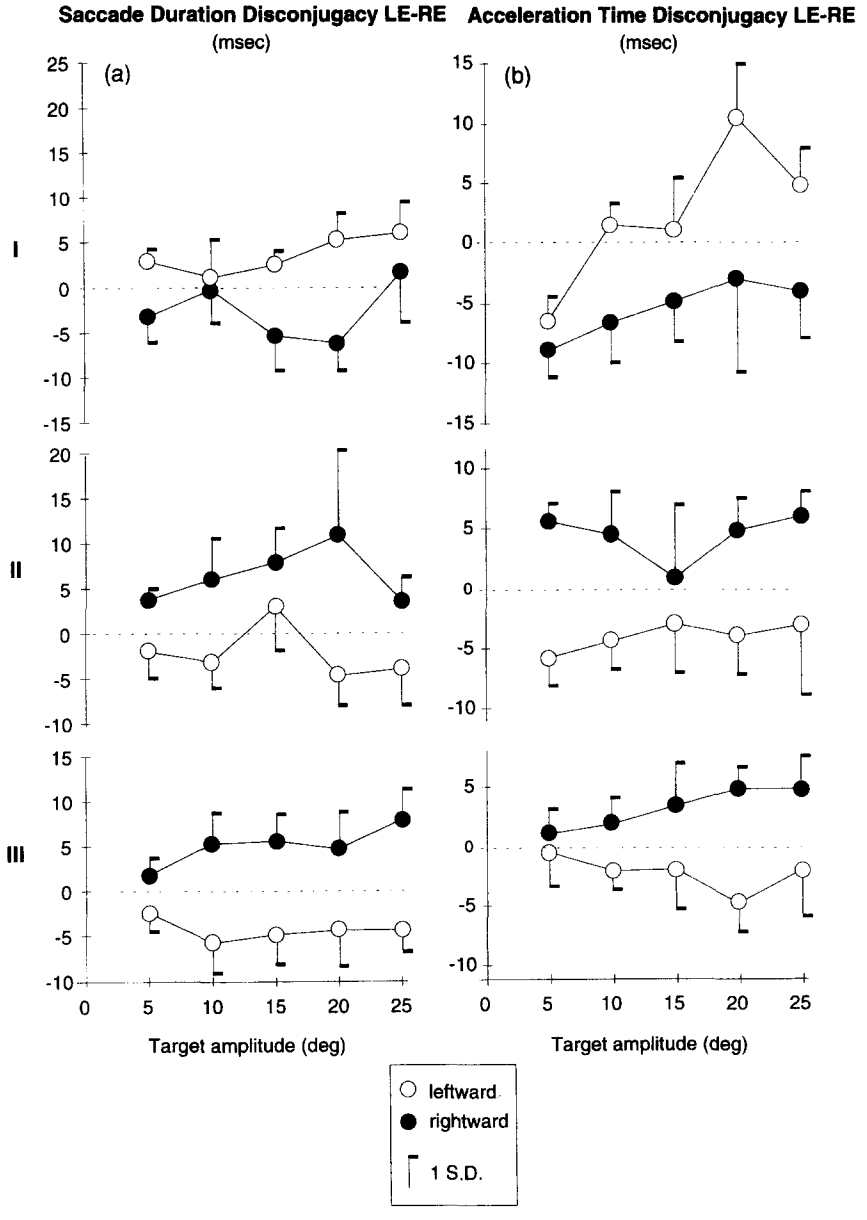

FIGURE 3. Saccade duration disconjugacy (a) and acceleration-time disconjugacy (b) of the saccades for groups I, II and III. Saccades from the two eyes were pooled together, but rightward (●) and leftward (○) directions are shown separately. Vertical bars indicate 1 SD.

than the corresponding saccades of the fellow eye. The average convergence at the saccade offset was 1.97 deg for group I, with maximum values larger than 4 deg.

For children belonging to group II, the dependency of the sign of the saccadic disconjugacy on the direction was opposite to that found in the group I: the abducting eye made significantly larger saccades than the fellow eye, producing a divergence of the eyes at the saccade offset. The saccade yoking was rather better than in children of group I, and the difference between the saccade amplitudes of the two eyes was reduced to a global mean value of 0.63 deg.

The same reversal of the temporal–nasal asymmetries between children of groups I and II can be observed in the peak velocity disconjugacy, shown in Fig. 2(b). In children of group I, the peak velocities of the abducting eye were on average about 61 deg/sec lower than those of the adducting one. The peak velocities of subjects belonging to group II were on average 20 deg/sec higher for the abducting eye than for the adducting one.

The reference values found in adults [Fig. 2(a, b), group III] were similar to those of group II: temporal saccades were larger (average 0.48 deg) and reached higher peak velocities (average 26.2 deg/sec) than the corresponding nasal saccades.

To complete the analysis of the disconjugacy of binocular saccades, we also studied the differences in the saccade durations of the two eyes [Fig. 3(a)].

For group I (top graph), saccades made by the abducting eye were longer than the corresponding adducting saccades (mean difference 3.11 msec), while for children in group II (middle graph) the duration was longer for the adducting saccades (mean difference of 4.29 msec). We also evaluated the differences in the duration of the acceleration phase of paired saccades, in order to understand if the origin of this reversed

behaviour was related to changes in the initial phase of the saccade (from the saccade onset to the peak velocity) or to changes in the final phase (deceleration phase, from the peak velocity to the saccade offset). Figure 3(b) shows that the sign of the acceleration-time disconjugacy in subjects of group I is opposite to that found in group II.

The group III graphs of Fig. 3 show the results of the same analyses for adult subjects, indicating that adducting saccades have longer duration [Fig. 3(a)] and a longer acceleration phase [Fig. 3(b)] than the abducting saccades of the fellow eye. The mean difference between durations of the adducting and abducting saccades was 4.93 msec.

In conclusion, the differences between rightward and leftward saccades were statistically significant in all the analysed parameters, showing that the asymmetries between temporal and nasal saccades are reversed in children belonging to group I with respect to those observed in subjects of groups II and III. The abducting saccades of subjects in group I have smaller amplitude, lower peak velocity, longer duration and a longer acceleration phase than the concomitant adducting saccades. In contrast, for subjects of group II, all these characteristics are reversed between adducting and abducting saccades, qualitatively fitting the results for the adult group.

Cyclopean accuracy of saccades

The accuracy of saccades was studied on the cyclopean eye position in order to rule out the contribution due exclusively to the disconjugacy and to enhance the effects of the conjugate neural control. Two parameters were used to characterize the difference between the position of the cyclopean eye and the position of the target: the cyclopean pulse position error (CPPE), evaluated as the absolute value of eye position at the saccade offset minus the absolute value of target position, and the cyclopean step position error (CSPE), evaluated in the same way at the end of the post-saccadic drift. Therefore, the CPPE is suitable for the description of saccadic overshoot and undershoot, while the CSPE indicates the under- or over-estimation of the target position.

The values of the CPPE in adults [Fig. 4(a)] were always negative, indicating a slight undershoot of the target position. The amplitude of the error increased with the amplitude of the target jump, but the relative error was always close to 10% (9.8% at 5 deg, 12.1% at 30 deg).

In children belonging to group I, the CPPE was positive for small target jumps (5 and 10 deg) and negative at larger amplitudes (15–25 deg), ranging between +72% and −30% of the target jump. For group II the CPPE was positive at 5 deg and negative for larger amplitudes, but with smaller relative values (5% to −20%) than in children of group I.

The large positive CPPE found at 5 deg target jumps (+3.61 deg for group I and +0.9 deg for group II) is in contrast with our findings in adults and with the typical values previously reported in literature, where the position error is consistently negative independently of the amplitude of the target jump. This means that children normally overshoot small target jumps and that saccadic undershoot is consistently observed only for target jumps larger than 15 deg. Figure 5 shows typical position and velocity profiles of abducting saccades in a subject belonging to group I (MM, 8 yr old).

The study of the CSPE in subjects belonging to groups I and II [Fig. 4(b)] showed that the error was consistently reduced from the saccade offset to the end of the post-saccadic drift. For each age group the sign of the CSPE presented the same dependency on the amplitude of the target jump already observed in the CPPE, suggesting that children overestimate the amplitude of small target jumps (5 and 10 deg) and underestimate larger target jumps. The differences between the CSPE and the CPPE in subjects belonging to group III was

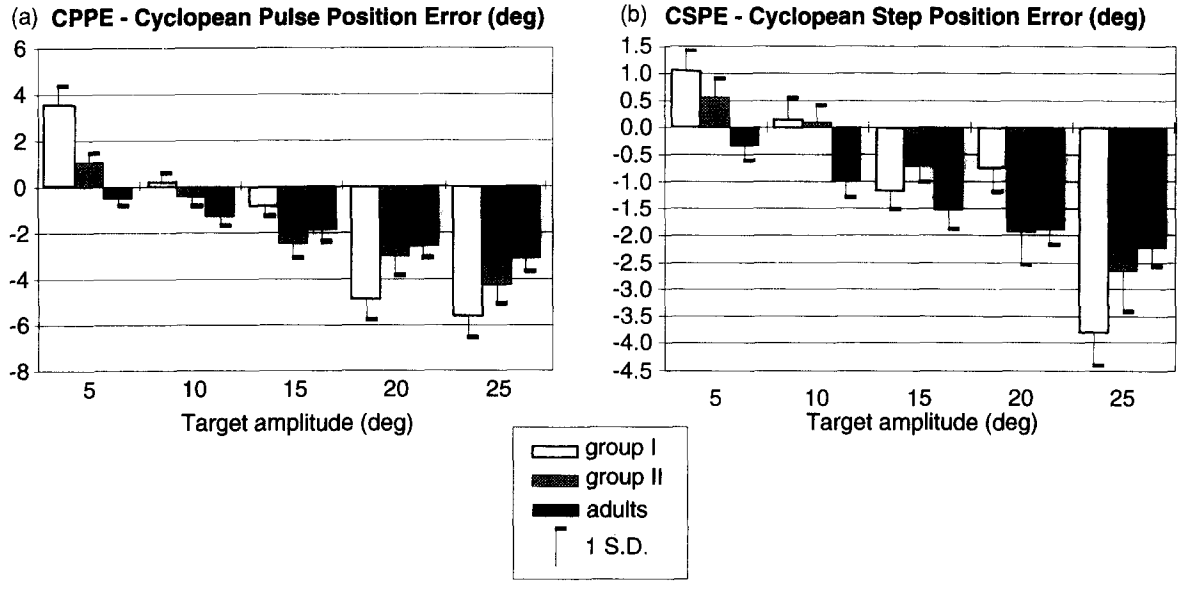

FIGURE 4. CPPE (a) and CSPE (b) for the three age groups. The cyclopean eye is the average of the left and right eye traces. Saccades followed by secondary saccades were rejected for the evaluation of the step position error. Vertical bars indicate 1 SD.

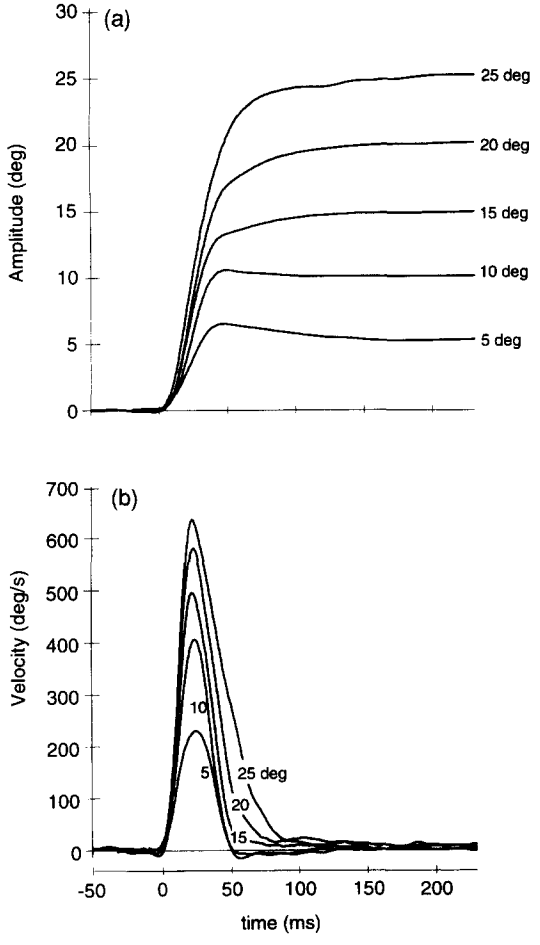

FIGURE 5. Eye position (a) and velocity (b) profiles of a typical family of abducting saccades (right eye traces) ranging from 5 to 25 deg (subject MM, 8 yr old, group I).

almost negligible, indicating very small post-saccadic drifts in adults.

Peak velocity and duration of saccades

Confirming the results reported by Accardo *et al.* (1992), we found that the peak velocity vs saccade amplitude relationship (saccadic main sequence) saturates in children for higher values than in adults.

The data were fitted with the following exponential function:

$$V_p = V_0[1 - \exp(-A/A_0)]$$

where V_p is the peak velocity, A the saccade amplitude, V_0 is the asymptotic saturation value and V_0/A_0 is the slope of the curve in the origin. Even though the values of these parameters showed large fluctuations with the age of the subjects, we found a statistically significant difference between the mean values in the three age groups.

Figure 6 shows the averaging of the peak velocities over all the orbital positions and over both saccade directions for each age group. The best-fitting values for the parameters V_0 and A_0, and the corresponding slopes V_0/A_0, were:

Group I $V_0 = 779.11$ deg/sec
$A_0 = 13.09$ deg
$V_0/A_0 = 59.52\,\text{sec}^{-1}$

Group II $V_0 = 627.73$ deg/sec
$A_0 = 11.08$ deg
$V_0/A_0 = 56.65\,\text{sec}^{-1}$

Group III $V_0 = 488.22$ deg/sec
$A_0 = 9.17$ deg
$V_0/A_0 = 53.24\,\text{sec}^{-1}$

The main sequence found in the reference adults is in agreement with most previous reports (Boghen *et al.*, 1974; Schmidt *et al.*, 1979; Bahill, Brockenbrough & Troost, 1981; Abel *et al.*, 1983; Collewijn *et al.*, 1988). The saturation of the main sequence (V_0) appears much higher in children than in adults, particularly in those of group I (+60% for group I and +29% for group II), although the slope in the origin (V_0/A_0) is only slightly higher in children (+12% for group I and +6% for group II).

Despite the higher peak velocities, the saccadic duration in children was longer for small target jumps, and increased by a smaller amount for larger amplitudes. The amplitude–duration relationship was described by the linear function

$$D = D_0 + D_1 A$$

where D is the saccade duration. The best-fitting values for the parameters D_0 and D_1 were:

Group I $D_0 = 55.94$ msec $D_1 = 0.49$ msec/deg

Group II $D_0 = 40.12$ msec $D_1 = 1.64$ msec/deg

Group III $D_0 = 28.70$ msec $D_1 = 2.59$ msec/deg

The group averages and SDs are shown in Fig. 7(a). It is evident that the higher peak velocities observed in children are not related to a general enhancement of the

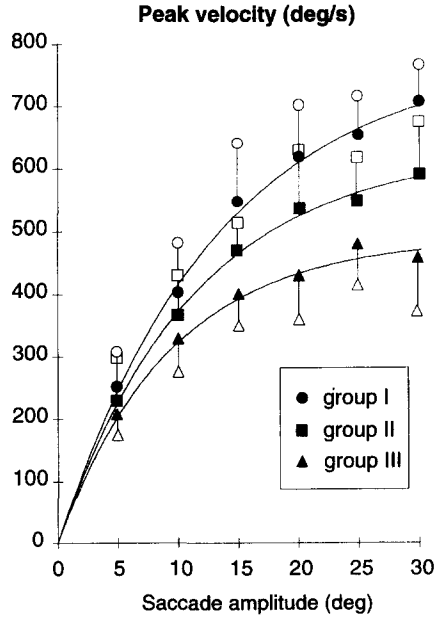

FIGURE 6. Peak velocity of saccades in children (groups I and II) and adults (group III) as a function of the saccade amplitude. Data from the two eyes in both leftward and rightward directions were pooled together. Solid symbols indicate the mean values; open symbols indicate 1 SD. The curves present the best exponential fit of the data for each age group.

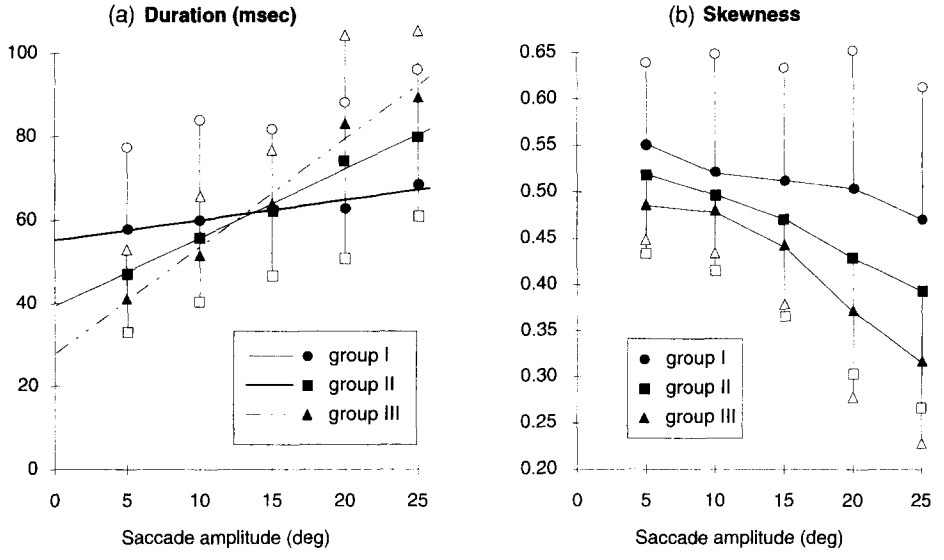

FIGURE 7. Duration (a) and skewness (b) of the saccades for the three age groups. Saccades from the two eyes in both leftward and rightward directions were pooled together. Solid symbols indicate the mean values; open symbols indicate 1 SD.

saccadic efficiency in terms of the time elapsed to reach the target position. In particular, small saccades in children exhibit larger durations than in adults: e.g. the mean duration of 5 deg saccades was 58.6 msec in group I, 48.9 msec in group II and 39.2 msec in adults.

However, at large amplitudes (15–25 deg) the saccade duration in children is comparable to or smaller than that found in adults, because of the exceptional flatness of the amplitude–duration characteristic in children. The relative increase of the saccade duration between 5 and 25 deg of amplitude is 68% in children of group II and only 16% in children of group I (see also the family of saccades in Fig. 5). For the reference adults the duration increase in the interval between 5 and 25 deg amplitudes is 124% with respect to the duration at 5 deg.

For a better understanding of the above-described behaviour, we studied the skewness of the saccades in children and adults, defined as

$$S = D_A/D$$

where D_A is the time interval of the acceleration phase, i.e. the delay of the peak velocity from the saccadic onset. A value of 0.5 means that the peak velocity occurs exactly at one-half of the saccade duration; higher values of skewness indicate that the position of the peak velocity is closer to the end of the saccade. The differences between children belonging to groups I and II were highly significant, showing [Fig. 7(b)] that in young children the peak velocity is reached after one-half of the saccade duration, while in older children and in adults the peak velocity occurs in the first half of the saccade. The total variation of the skewness over the whole range of saccade amplitudes is significantly smaller in children of group I (group I, 0.08; group II, 0.14; group III, 0.18).

DISCUSSION

Comment on methods

In many recent studies on adults, very precise and accurate measurements of horizontal saccades were performed with instrumentation based on the scleral search coil technique (Robinson, 1963; Collewijn, Van der Mark & Jansen, 1975). Unfortunately, this type of recording system is not suitable for extensive studies on children, since it is semi-invasive. This limitation in the use of precise instrumentation results in a scarce availability of results on the binocular coordination of saccades in young subjects, since it is very difficult to obtain stable and accurate calibration for both eyes with other measurement techniques. For these reasons, we adopted the infrared limbus-tracking technique, using a device appositely designed by our group for accurate wide-range measurements in children and then processing the recorded data with precise non-linear calibration algorithms. To validate the precision and stability of our instrumentation, we analysed binocular saccades in four adult subjects and compared the results with existing documented data. Although small discrepancies due to different experimental paradigms were observed, our results in adults are in agreement with many previous reports.

Cyclopean saccade accuracy and version drift

For adult humans, we reported in Fig. 4 a negative CPPE (target undershooting), almost linearly increasing at a rate of about −11% of the saccadic amplitude, confirming previous findings on the undershooting of human primary saccades with jumping targets (Becker & Fuchs, 1969; Becker, 1972; Henson, 1978; Prablanc, Masse & Echallier, 1978; Pelisson & Prablanc, 1988; Lemij & Collewijn, 1989). The version drift was very small, so that the CSPE approximately coincided with the CPPE. This means that jumping targets produce in adults a rather inaccurate estimation of the "desired change of eye position", as shown by the CSPE. Conversely, in

groups I and II, the CPPE was larger than in adults and was associated to exaggerated conjugate drifts rather than to an inaccurate estimation of the "desired change of eye position", as confirmed by the smaller CSPE. In conclusion, both groups of children exhibited an absolute CSPE similar to or even better than that found in adults. This means that the basic mechanisms assuring the metricity of the saccadic system and, therefore, producing orthometric saccadic steps, work as well in children as in adults; at the same time, however, these results show that the optimization of the saccadic pulse waveform is poor in children, and that it improves with their age, as the higher CPPE values were found in children of group I, aged from 5 to 10 yr.

The analysis of the dependency of the CPPE on the target amplitude can help to understand the origin of such low optimization. In subjects of groups I and II the smaller CPPE (Fig. 4) was found for target displacements around 10 deg, where it was reduced to absolute values consistently smaller than 0.5 deg. However, this value of the CPPE changed for larger or smaller target amplitudes, with variations of about −27% of the target displacement with respect to 10 deg for group I, and about −45% for group II (Fig. 4). Consequently, target jumps smaller than 10 deg were overshot, while the larger ones were undershot. Since we evaluated the CSPE as the position error at the end of the post-saccadic drift when no secondary saccades occurred, the amplitude and the direction of the cyclopean drift are defined by the difference between the CSPE and the CPPE. Therefore, the version drift in children was backward for small target amplitudes, almost zero for target jumps of about 10 deg and onward for larger amplitudes.

Why are saccades in the 10 deg range privileged in children? The oculomotor system has a non-linear behaviour, particularly evident during high-speed, transient motions of the eyes: it is due to phasic saturation or interdiction (zero-frequency discharge) of burst and burst-tonic activities in premotor neurons and motoneurons, and to the non-linear viscosities of the plants. To produce the correct tonic–phasic innervation, matching the plant characteristics for any saccadic size at each orbital position, the oculomotor system must therefore be able to account for the current "efficiency" of the phasic activities and modify on-line the temporal characteristics of the saccadic commands according to the current task (Inchingolo, 1986): in this way centrifugal saccades are programmed with longer durations and smaller peak velocities than centripetal saccades. This can be done automatically by an internal model of the plants and the premotor circuits (Inchingolo & Bruno, 1994), provided that the distributed parameters of this model were previously set by an appropriate learning period. The same efficiency-related adjustments must be applied for movements of different sizes, because they are associated to unequal mechanical activities of the agonist and antagonist muscles and, therefore, to different efficiencies of the phasic activity. In adult subjects the optimization seems to work over all the oculomotor range, since they learn the complete behaviour of the system by experience, and thus they can fix the internal model almost completely. Saccades of any size are in fact largely used by adults in normal life: small saccades are necessary to read, write and to do many precise manual tasks requiring visual feedback, while large saccades are used, even combining them with head movements, to produce large gaze shifts. Conversely, children do not experience large eye movements, since they usually accomplish large gaze shifts almost exclusively with head motions, nor do they experience very small eye movements, since they (in particular the youngest ones) do not read, do not write and do not make precise hand tasks. A consistent enhancement of the saccadic accuracy and precision for intermediate amplitudes (about 10 deg) in children is therefore plausible. When a new stimulus for larger or smaller ocular saccades is presented, they use their default optimization, which is appropriate only for saccades of the well-tried size. For smaller saccades, where efficiency is higher, the amount of phasic activity is excessive and produces overshooting saccades followed by drift backward; conversely, the same amount of phasic activity is inadequate for larger saccades, characterized by lower efficiency, and produces undershooting saccades with drift onward. Furthermore, as a consequence of this default setting of the premotor circuits and, in particular, of the local feedback loop (Robinson, 1975), the programmed saccadic duration in children is too long for small amplitudes, and too short for large ones. For this reason the amplitude–duration characteristics of both the age groups exhibit abnormally small slopes, exaggeratedly high intercepts on the duration axis, and cross the correspondent characteristics of adults at the amplitude of about 10 deg. This also explains the finding that saccades of almost any size are almost symmetrical, particularly for very young children, as shown by the skewness values close to 0.50 (Fig. 7). A sign of the progressive setting of the internal model associated to the visuo-motor experience during growth could come from the comparison of the amplitude–duration, the skewness and the CPPE characteristics observed in the two groups of children: passing from group I to group II, in fact, both the slope and the intercept values changed towards the typical values found in adults.

Saccade disconjugacy and vergence drift

It is well known that saccades of the two eyes are slightly different. In adult humans the saccades of the abducting eye usually have larger amplitude, larger peak velocity, shorter duration and smaller skewness than the saccades of the fellow eye (Collewijn *et al.*, 1988; Zee *et al.*, 1992). These differences between the nasal and temporal saccades produce consistent intra-saccadic divergence (Kapoula *et al.*, 1987) of up to several degrees, which decrease to about 0.3 deg at the offset of each saccade larger than 5 deg (Collewijn *et al.*, 1988). Similar intra-saccadic vergence patterns were observed in subjects belonging to groups II and III, although in children the net vergence change at the saccade offset was quantitatively larger than in adults. In contrast, younger

children belonging to group I exhibited a reversal of all those characteristics: in both directions the saccades of the abducting eye had smaller amplitude, smaller peak velocity, longer duration and larger acceleration time than the saccades of the abducting eye (see Figs 2 and 3). Furthermore, the eyes transiently converged during saccades and diverged slowly back with the disconjugate post-saccadic drift.

The source of the transient divergence has been generally searched in the mechanical asymmetries of the orbital plants. Collewijn *et al.* (1988) recalled the measurements of Collins, Carlson, Scott and Jampolsky (1981), who found that the stiffness when the left eye was rotated in the nasal direction was about 11% greater than the stiffness when the same eye was rotated in the temporal direction. Zee *et al.* (1992) supposed that the two eye plants, modelled as two-poles and one-zero elements, exhibit slight differences (few msec) between the corresponding short-time-constant poles.

Why do very young children show a reversal of all the characteristics of the saccadic yoking? Are all the parameters of the plants and of the premotor structures different during the first years of life or can, alternatively, just few different parameters condition all these characteristics? An answer to this question would have a general value, since it could help to explain the variability of many details of the saccadic waveforms in normal and pathological humans.

The large post-saccadic drifts found in children of group I indicate the lack of an accurate compensation of the dynamic properties of the plants: since saccadic waveform is strictly dependent on the amount of phasic activity sent to the muscles, a wrong adaptation of the pulse-step of innervation could be responsible for the unusual disconjugate characteristics observed in very young children.

The post-saccadic drift in each eye can be modelled with the step-response of a linear system with one zero and one pole:

$$H = \frac{1 + sT_z}{1 + sT_p}$$

where T_z and T_p are the time constants of the zero and the pole respectively. If $T_z = T_p$, the above expression is equal to 1, and the eye will not drift at all. When $T_z > T_p$ the eye will drift backward with time constant T_p and a size A_D approximately equal to

$$A_D = A_S \frac{T_p - T_z}{T_p}$$

where A_S is the amplitude of the saccadic step. When $T_z < T_p$ the eye drifts onward with the same time constant and a size still given by the above expression.

Since disconjugate post-saccadic drift components were found in children, the zero-pole matching of function H must be different for the two eyes. The H functions of the two eyes affect the saccadic waveforms, smoothing and prolonging the saccade when $T_p > T_z$, or enhancing its speed and shortening its duration when $T_z > T_p$.

To nullify the effect of these functions on the saccades of children belonging to group I, we identified the values T_z and T_p, and therefore we filtered each saccade with the inverse function

$$H^{-1} = \frac{1 + sT_p}{1 + sT_z}.$$

The value of the pole was detected by fitting the post-saccadic drift with an exponential function; the value of the zero was set by computing the amount of pulse-step mismatch, according to the above reported expression for A_D. For example, from the largely disconjugate, rightward saccades reported in Fig. 8, we identified $T_z = 86$ msec for both eyes, $T_p = 100$ msec for the right eye and $T_p = 76$ msec for the left eye. These values of T_p can be ascribed to the visco-elastic properties of the plant: with this assumption, the zero-pole couple of the H functions could originate from the visco-elastic elements of the muscles (pole) and the pulse-step innervation command (zero) or can be produced by the uncompensated sliding components of force due to orbital tissues (Inchingolo & Bruno, 1994). In the first case, the inverse filtering of the saccadic waveform is equivalent to the inverse reconstruction of the pulse-step cyclopean innervation, to the synthetic generation of a couple of disconjugate pulse-steps, each one producing a zero equal to the pole of the corresponding eye, and to the application of such disconjugate control signals to the two plants. In the second case, the manipulation of the saccadic waveforms is equivalent to the application of a couple of disconjugate slide-step compensation stages in the premotor circuits to the two eyes.

The results obtained with this artificial disconjugate compensation of the two eyes were surprisingly clear. In most cases the intra-saccadic vergence reversed from a quick and large convergence to a quick and smaller divergence–convergence [Fig. 8(c)], as usually seen in normal adults, proving that this is a basic disconjugate property of the eyes, probably due to the small time constants of the plants. All the post-saccadic drift disappeared [Fig. 8(a)] and both the position and velocity profiles showed a higher degree of yoking [Fig. 8(b, d)].

In conclusion, we showed that the large disconjugacy of saccades found in children is mainly due to the lack of disconjugate compensation of the plants. Since many recent studies on human adults and primates reported even large disconjugate pulse-step adaptations (Inchingolo *et al.*, 1991; Kapoula *et al.*, 1987, 1990, 1994), our findings suggest the following possibilities: (i) the disconjugate drift adaptation mechanism is poor in children and improves during growth; (ii) the asymmetry in the mechanical properties of the plants is very large in children, exceeding the range of disconjugate adaptation, and is reduced during growth. Of course, a combination of the two possibilities would be more realistic.

This study also suggests that in any research, to make reliable comparisons of saccade characteristics between different samples of subjects, all the recorded saccades should be normalized with the method proposed here, in order to eliminate the idiosyncratic differences due to the

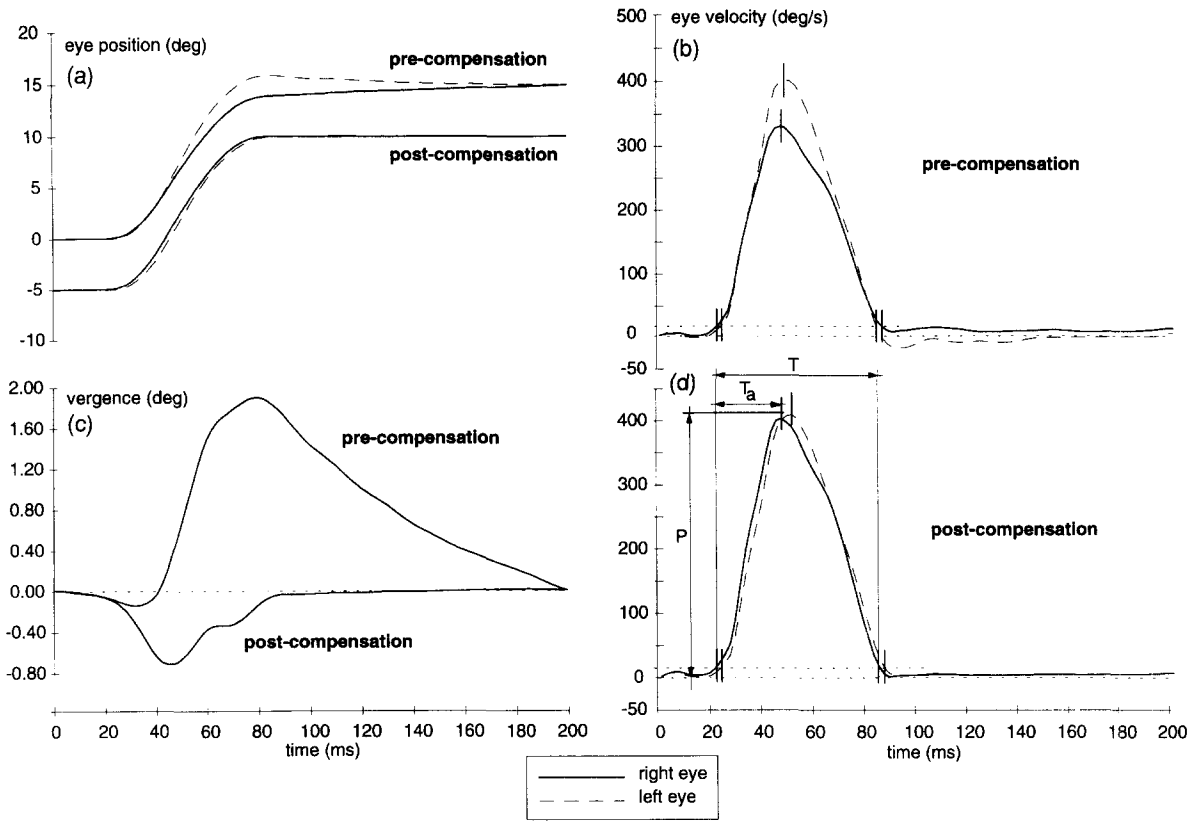

FIGURE 8. Effects of the inverse filtering of a couple of saccadic waveforms using a zero-pole function. (a, c) The eye position traces (a) and the vergence trace (c) before (pre-compensation) and after (post-compensation) the filtering. (b, d) Velocity traces of the original (b) and filtered (d) saccades; the vertical marks indicate the thresholds used by the saccade identification algorithm. *P*, *T* and T_a indicate the peak velocity, the duration of the saccade and the duration of the acceleration phase respectively. See text for details.

post-saccadic drifts, that, although smaller than in children, are always present.

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